Modern Taxonomy and Its Relation to Geography*

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Taxonomy in the last seventy-five years has had increasingly close connections with geography, but the subject is so vast that only a small portion of the field can be covered at this time. The most that can be done is to review some of the geographical theories that have been in the light for two decades or more, and with which we all are more or less familiar. These subjects are so intertwined that separate discussion of any of them is difficult and all of them are but loose ends of the tangled thread that represents our fund of knowledge of plant geography.

As to geographical location, we are practically astride the terminal glacial moraine which runs the length of Long Island, and which was a collecting ground for Asa Gray when he was associated with Torrey in New York. Much ink has flowed on the subject of glaciation and its effect on plants since Gray published his remarkable report on the similarities of the flora of eastern Asia and eastern North America, in 1859. This date, which coincides with that of the "Origin of Species," was only eight years before the founding of the Torrey Club, which can therefore be said to have occupied practically the whole period of modern biology. Gray's remarks were based on a collection by Charles Wright, who is also well-known for his collections in Cuba and for those in his own part of the Torrey Club Range, in Hartford, Connecticut.

As every taxonomist knows, the genera and even many species which we find in our southern Appalachians are the same as those of the mountains of western China and of Japan. The following quotations are from Gray's paper, Amer. Acad. Arts and Sci. Mem. 6: 1859: "The fundamental and most difficult question remaining in natural history is here presented; the question whether this actual geographic association of congeneric or other nearly related species is primordial and therefore beyond all scientific explanation, or whether even this may be to a certain extent a natural result. The only noteworthy attempt at a scientific solution of the problem is that of Mr. Darwin and Mr. Wallace,[1] partially sketched in their short papers, 'On the Tendency of Species to Form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection'" (p. 443).

"At length, as the post-tertiary opened, the glacier epoch came slowly on—an extraordinary refrigeration of the northern hemisphere, in the course of ages carrying glacial ice and arctic climate down nearly to the latitude of the Ohio. The change was evidently so gradual that it did not destroy the temperate flora,

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[1] Journ. Linn. Soc. (Zoology). 3: 45. 1858.

at least not those enumerated above as existing species. These and their fellows, or such as survived, must have been pushed on to lower latitudes as the cold advanced . . . , portions of which, retreating up the mountains as the climate ameliorated and the ice receded, still scantily survive upon our highest Alleghenies, and more abundantly upon the colder summits of the mountains of New York and New England."

" . . . perhaps the most interesting and most unexpected discovery of the expedition is that of two strictly Eastern North American species of this order [Berberidaceae],—each the sole representative of the genus,—viz. *Caulophyllum thalictroides,* and *Diphylleia cymosa,* of Michaux . . . are we to regard them as the descendants of a common stock . . . or are we to suppose them independently originated in two such widely distant regions?" (p. 380).

"*Smilacina* (*Majanthemum*) *bifolia* extends around the world, but under three pretty well marked geographical varieties:—the European, which extends to eastern Siberia; the var. *Kamtschatica,* which replaces the former on the Pacific Siberian coast, in Japan, and in North America west of the Rocky Mountains; and the var. *Canadensis,* throughout all the northern part of this country east of the Mississippi and the Rocky Mountains" (p. 414).

These quotations, it will be seen, are important from three points of view in our modern taxonomy: 1) affirmation of the idea of evolution by the natural selection of variations, 2) the negation of the bicentric origin of species, 3) recognition of a holarctic Cretaceous flora of common origin, and its disruption by the Glacial period.

And we arrive here at one of our first taxonomic difficulties. Shall these geographic variants, which Gray showed to be of common origin, be classified as a single species or shall they be segregated as separate species? This important question we cannot decide. As Weatherby[2] has noted: "so long as we have to rely on judgment at all, the accuracy and soundness of any taxonomic category, definition or no definition, will be in direct proportion to the accuracy and soundness of judgment of the individuals who apply it." The pendulum swings this way and that over periods of time. For example, the yellow lady's slipper (*Cypripedium pubescens*) of eastern United States has long passed as distinct, but only recently Correll[3] has with some justification treated it as a variety of the Eurasian *Cypripedium Calceolus.* The common brake of eastern North America, long held as a separate species under the name *Pteridium latiusculum,* has recently been returned by Tryon to its very old status as a subdivision of the wide-spread *Pteridium aquilinum.* And in Rhodora for this very month of June we find the common water-plantain, which through later years we have been patiently calling *Alisma subcordata,* blooming forth after

[2] Rhodora **44**: 160. 1942.

[3] Harvard Bot. Museum Leaflet **7**: 1-18. 1938.

a fashion as a small-flowered variety of the Eurasian *Alisma Plantago-aquatica*. Not only are species and their subdivisions the product of opinions of individuals, but the same is true of the limits of genera and of higher groups. Not much is to be gained by a painful recital of the infinite variation of nomenclature under present conditions; it is much more illuminating to review the geographic conditions which have made or should make a background for nomenclature.

This problem of glaciation in eastern North America has been ably treated by Professor Fernald. He has shown that many species of restricted distribution in Western Newfoundland, in the Gaspé Peninsula of eastern Quebec, and in some areas adjacent to the Great Lakes, are ancient plants (in contradistinction to Willis' "Age and Area" hypothesis) that have persisted in places not covered by the Wisconsin stage of the Pleistocene glaciation. The vegetation of the glaciated area we may presume to have been obliterated during the ice age, and since the deposits of the coastal plain are of comparatively recent origin (chiefly marine) the uplands of the southern Appalachians and the Ozark Mountains remain as areas from which the flora now inhabiting the coastal plain has probably been derived. These various areas are shown in detail in Fernald's[4] recent work on the Virginia coastal plain.

Species which cover the three main areas (Appalachian uplands, glaciated area, and coastal plain) often show marked divergences in structure in these individual areas, and constitute geographic varieties, which if the variations increased (according to the Darwinian interpretation mentioned in my opening paragraphs) might become distinct species. The Appalachian plateaus still harbor many species of the coastal plain, and from my own observations on the vegetation of the barrens of Middle Tennessee, it seems probable that such plants as *Panicum meridionale, Rynchospora macrostachya, Scleria reticularis,* and *Eleocharis microcarpa* have moved into the Great Lakes area from the siliceous uplands of Tennessee and Kentucky through Indiana, as we may infer from isolated occurrences in the last named state. The bicentric range of *Lilaeopsis carolinensis* in south-eastern United States and in the Argentina region of South America is also shown. A similar disrupted distribution is common in other groups, especially in the Cyperaceae, and is well shown in a number of species of *Eleocharis*. Whatever may be the geographical explanation, the problem of correlating published varieties and other subspecific units in variable species with such bicentric ranges is well-nigh insuperable; it is perhaps the most cogent argument for the non-recognition of varieties.

We may now turn attention to a recent publication of extraordinary interest by J. C. Willis,[5] the author of "Age and Area." This work, entitled: "The

[4] Rhodora 42: 367. 1940.

[5] Cambridge University Press. England. 1940. 200 pp. Quotations by permission of The Macmillan Company, publishers, U. S.

Course of Evolution by Differentiation or Divergent Mutation," is a negation of evolution by the natural selection of variations as propounded by Darwin and Wallace and affirmed by Asa Gray. The idea is not an original one, but is based largely on what Guppy called "differentiation," in his work on the vegetation of tropical islands. The eleventh chapter leads out, "Natural selection, being a common phenomenon of everyday experience, has exercised such a fascination that it has to a notable extent inhibited people from trying properly to think out how a principle, whose essence is competition with partial escapes into usually temporary success every now and then by improved adaptation, can produce the ordered arrangement, taxonomy, and morphological or structural uniformity with which we are familiar" (p. 103). Many, if not most or even all, of the characters of distinction that mark families, sub-families, and even smaller groups, are such that they can have no serious value upon the physiological side which is the only one that matters from the point of view of natural selection or gradual adaptation. These mutations are assumed by Willis to require long periods of time and to occur infrequently. "If one suppose a genus to give off new species more or less in proportion to the area that it covers (which again will be more or less in proportion to its age among its peers), it is clear that all the offspring will carry a large proportion of the characters of the parent, and that therefore while offspring arising near together will be most likely closely to resemble one another, there is no reason why a close resemblance should not arise with a wide geographical separation" (pp. 155, 156). "It will commonly be found, in studying the distribution of the species of a genus, especially if it be of small or moderate size, that they are more densely congregated toward the centre of the distribution of the genus, and fall off gradually toward the edges, so that when one draws a line round the outermost localities of each species one obtains a picture not unlike that which is called a contour map by geographers . . . " thus, Willis illustrates the distribution of the species of *Ranunculus* found in New Zealand (pp. 149, 150). "Here one finds 'wides' (as I have called the species which have a dispersal outside the country in question) occupying the whole area of the islands of New Zealand, and also reaching eastwards to the Chatham Islands, 375 miles away . . . The endemics are evidently crowded together rather south of the middle of the South Island, whilst they fade out completely before the north end of the North Island is reached . . . The general impression that one gains from a map like this is that the genus *Ranunculus* entered New Zealand probably from the south, and at some place in the southern half of the South Island, where the incoming species began giving rise to endemics, and on the average each species, wide or endemic, spread to the distance allowed by its age, and suitability to the conditions with which it met."

We now come to a region which has played a prominent part in taxonomy, the Galapagos Islands and the adjacent coast of South America. These islands were visited by Darwin in 1835, and upon the variations of birds and tortoises from island to island, as well as upon the plants which were named by the younger Hooker, were laid the foundations of evolution by geographic isolation. The plants were briefly discussed by Darwin in the "Origin of Species" (p. 349): "Dr. Hooker has shown that in the Galapagos Islands the proportional numbers of the different orders are very different from what they are elsewhere. All such differences in number, and the absence of certain whole groups of animals and plants, are generally accounted for by supposed differences in the physical conditions of the islands; but this explanation is not a little doubtful. Facility of immigration seems to have been fully as important as the nature of the conditions.

"Many remarkable little facts could be given with respect to the inhabitants of oceanic islands. For instance, in certain islands not tenanted by a single mammal, some of the endemic plants have beautifully hooked seeds; yet few relations are most manifest than that hooks serve for the transportal of seeds in the wool or fur of quadrupeds. But a hooked seed might be carried to an island by other means; and the plant then becoming modified would form an endemic species, still retaining its hooks, which would form a useless appendage . . . trees growing on a continent, might, when established on an island, gain an advantage over other herbaceous plants by growing taller and taller and overtopping them. In this case, natural selection would tend to add to the stature of the plant, to whatever order it belonged, and thus convert it into a bush and then into a tree."

It is interesting to note in this connection that the only genus of plants now recognized as endemic to the Galapagos Islands is *Scalesia*, which is bushy or sometimes nearly herbaceous in the lower parts of the islands, but some species become large trees where the moisture is more plentiful. Stewart in 1911 estimated that 40 percent of the plants (varieties and forms being included in the count), were endemic, but as in the case of the birds, the larger percent of the endemic plants occur in a few groups. Many supposed endemics, furthermore, have been recently found on the desert coasts of Ecuador and northern Peru; these areas have a climate strikingly similar to that of the Galapagos Islands, and together with the islands seem to form a marked geographic province. Taxonomic problems which vex the botanist have cropped up among the ornithologists. For example, J. Huxley writes of Swarth (quoted by Goldschmidt in "The Material Basis of Evolution," p. 209), "after classifying them [the Galapagos finches] into five different genera with over thirty species and subspecies, . . . it would be almost as logical to put them all in one genus and species." So far as the Galapagos are concerned the astounding extremes of

climate which occur in the same or adjacent localities in both islands and the mainland may perhaps become as important to taxonomists as the question of isolated land masses. Nor do these examples complete the difficulties of the taxonomic picture. The coasts of Ecuador and Peru have been visited in a desultory manner by botanists for over two centuries: Feuillee, Cavanilles, Ruiz, Pavon, Humboldt & Bonpland, Hartweg, Andersson, Spruce, and Weberbauer. New species were described bountifully, more frequently than not without any references or comparisons with what had been described before. In this repect there is still much room for improvement in taxonomy.

This brings us to the last item, the question of taxonomy in respect to the organism as a whole. A number of recent papers might be mentioned, but none, it seems, quite comes up to the recent Memoir of the Torrey Club by Stebbins, "Studies in the Cichorieae; Dubyaea and Soroseris, Endemics of the Sino-Himalayan Region." Such a treatment includes taxonomy, anatomy, cytology, morphology of pollen grains, and probable phylogeny, especially in relation to the geography of the species. If taxonomy in general were treated with such care, many of our most distressing problems of nomenclature would vanish.

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